

DESCRIPTION AND DISTRIBUTION OF *ACACIA MACRACANTHA*
HUMB. ET BONPL. EX WILLD. (LEGUMINOSAE, MIMOSOIDEAE) IN
NORTHERN CHILE

DESCRIPCION Y DISTRIBUCION DE ACACIA MACRACANTHA
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EL NORTE DE CHILE

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ABSTRACT

The widespread neotropical legume tree *Acacia macracantha* Humb. & Bonpl. ex Willd. is reported from several isolated habitats in the northern tip of Chile (I Region), where it reaches the austral endpoint of its natural distribution along the Pacific coast of South America. Hitherto, *Acacia caven* (Mol.) Mol. has been considered the only *Acacia* native to Chile. However, although much rarer, *A. macracantha* seems to deserve the label "native to Chile" as well. Variability in size and shape of pods, leaves, and stipular spines of *A. macracantha* has led to its being split into numerous regional taxa, many of which appear to be of dubious merit. Brief discussion is made of the relationship between *A. macracantha* and several closely related taxa from Peru, the Galapagos Islands, Central America, and especially with *A. aroma* Gill. ex Hook. & Arn. of northern Argentina.

RESUMEN

Históricamente, una sola especie de *Acacia* se considera nativa en Chile —el espino, *Acacia caven* (Mol.) Mol. Sin embargo, se nota la presencia de *Acacia macracantha* Humb. & Bonpl. ex Willd. en varios hábitats húmedos en el extremo norte de Chile (I Región). Se trata de una simple continuación geográfica de la zona de repartición de esta especie en la costa del Pacífico desde el norte del Ecuador.

Morfológicamente, el material chileno corresponde al tipo de *Acacia macracantha*, oriundo de Guayaquil, Ecuador, y no es distinguible del material peruano. Después de una descripción detallada del material chileno, se considera la confusión taxonómica que resulta de la amplia variación y distribución biogeográfica de la especie, y de la hibridización introgresiva que se nota entre ésta y varias otras especies del mismo subgénero *Acacia* Vassal (=serie *Gummiferae* Benthams). La relación entre *A. macracantha* y *A. aroma* de Argentina se discute en particular.

KEYWORDS: *Acacia macracantha*, *A. caven*, *A. aroma*, Leguminosae, distribution, description, Chile.

INTRODUCTION

Acacia caven (Mol.) Mol. has usually been considered the only *Acacia* native to Chile (Muñoz 1959; Follmann and Matte 1963;

Rodríguez *et al.* 1984; Marticorena and Quezada 1985). Yet in the subtropical river valleys of the northernmost 1st Region occurs a second species, *Acacia macracantha* Humb. & Bonpl. ex Willd. (Reiche 1905). Only collected a handful of times in northern Chile between 1880 and 1955, this second species has been considered adventive in Chile, along with several intentionally-introduced acacias that occasionally escape

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cultivation in the, 1st and 2nd Regions [e.g., *Acacia karroo* Hayne, *A. farnesiana* (L.) Willd., and *A. visco* Lorentz ex Griseb]. Yet unlike these three species, and in sharp contrast to *A. caven* itself (Ovalle, *et al.* 1990), *Acacia macracantha* in northern Chile occurs in precisely comparable habitats as the nearest populations of the same species along the Pacific coast of southern Peru. Furthermore, just as in Peru, Ecuador, Colombia and Venezuela, *A. macracantha* in northern Chile occurs exclusively in warm subtropical river valleys, in areas subject to frequent disturbance by man. Like *Caesalpinia spinosa* (Mol.) Kuntze, with which it always grows in association, *A. macracantha* is heavily exploited for firewood, and consequently very rare in Chile. Yet the populations formed by the two species appear quite natural, amounting in all likelihood to remnants of stands that were much larger in pre-Colonial times. In this paper, I give a description and list all known collections of *A. macracantha* as it occurs in Chile, and briefly discuss the geographical distribution, ecological amplitude and numerous phenotypic variations of *A. macracantha*, commenting on some of the taxonomic problems that surround it at the present time. I propose that *A. macracantha* merits the label "native to Chile" no less than *Acacia caven*.

GEOGRAPHICAL DISTRIBUTION AND HISTORICAL TAXONOMY

The binomial *Acacia macracantha* was based on material collected in Guayaquil, Ecuador (Willdenow 1806). Today, this species is widespread in inter-tropical America, including the Caribbean region (Adams 1972; Correll and Correll 1982; Liohier 1985; Barneby and Zanoni 1989), southern Mexico (McVaugh 1987), and the southern tip of Florida (Ward 1967). In South America, *A. macracantha* is found near the Atlantic coast of Venezuela (Steyermarck and Huber 1978; Cárdenas and de Martino 1989), along the Pacific ridge from Ecuador to northern Chile and in several intermontane valleys in Peru and Ecuador (Weberbauer 1911; Macbride 1943). Its presence in Bolivia and Argentina has not been well established and is in fact somewhat doubtful.

Along with *Acacia caven*, *Acacia*

macracantha belongs to subgenus *Acacia* Vassal (= series *Gummiferae* Benthams), of which there are about fifty species in the warmer parts of the Americas and some 30-40 species in Africa (Benthams 1875; Vassal 1972; Guinet and Vassal 1978; Elias 1981; Rico Arce 1980, 1984). Despite its considerable ecological importance, *A. macracantha* has never been studied on a continental or inter-continental scale. Consequently, there is confusion concerning its taxonomic and biogeographic delimitations. A similar situation prevails in other widespread members of the subgenus, such as *A. farnesiana*, *A. erioloba* E. Mey., *A. karroo*, *A. nilotica* (L.) Willd. ex Del., *A. tortilis* (Forssk.) Hayne, and several others (see Brenan 1970; Ross 1979; Seigler and Ebinger 1988). Of more relevance to Chile, the taxonomy of *Acacia caven* is also far more complex than is usually recognized locally (Cialdella 1984; Aronson 1991).

The material of *A. macracantha* found in northern Chile fits Willdenow's (1806) description of the type collected by Humboldt and Bonpland (Field Mus. neg. 1278 ex B!) and match what appears to be the most commonly accepted concept held for this species in its area of major concentration, i.e., the Caribbean region and Mexico. There remains, however, some confusion concerning the size and shape of the stipular spines, and some other parameters, as discussed below.

MATERIALS AND METHODS

Following visits to the herbaria of the Museo Nacional de Historia Nacional (SGO) and the Universidad de Concepción (CONC), I visited all the sites in the 1st Region of northern Chile from which *Acacia macracantha* has been collected in the past. This was accomplished in January - February, 1989. During the same field trip, I collected the same species and observed its habitat as far north as Arequipa, Peru. Finally, I consulted the major Latin American floras and all recent taxonomic treatments of *Acacia macracantha*, and examined specimens deposited at herbaria in Argentina (BA, CTS, CORD, LIL, SI), Bolivia (LPB), Brazil (MBM), and England (K). Additionally, I made several collections of the closely related *Acacia aroma* Gill. ex Hook. et Arn. and examined numerous herbarium

collections there of from various parts of northern Argentina.

RESULTS

DESCRIPTION OF *ACACIA MACRACANTHA* IN CHILE

Based on the herbarium specimens available, the Chilean material of *Acacia macracantha* can be described as follows:

Tree 2.5-6 m; all parts of plant pubescent; *leaves* bipinnately compound, 15-20 cm long, 30-70 mm wide, with 24-40 pairs of pinnae; *petioles* 5-12 (rarely 15) mm long; *pinnales* 2-3 mm long, *petiolar nectaries* slightly stalked, 0.1-0.3 mm across, one near base of petiole, several more at junctions of pinnae pairs on apical half of leaf. Nectaries tend to shrink when dry and appear sessile. When dry, they appear round to oval, with a concavity in the middle. *Spinescent stipules* (hereafter "spines") are small on young twigs (up to 5 mm), but up to 6.5 cm on older twigs and branches. Larger spines flattened and tapering, thus sword-shaped when fully developed and widely divergent, like bulls' horns. In cross-section, younger spines round to oval, the larger one rhomboid or nearly diamond-shaped. *Inflorescence* a dense globular capitulum 6-8 mm across, solitary to few in the axils of leaves, yellow or pale orange; *peduncles* 20-25 mm long, pubescent. *Flowers* hermaphroditic, 0.7-1.2 mm long, typical of Mimosoideae: actinomorphic, valvate prior to anthesis. *Fruit* a straight or rarely slightly curved legume, with edges entire, 60-85 mm long, 7-12 mm wide, 3-5 mm thick, compressed, striate, pubescent, with brown pericarp and white or cream-colored dry mesocarp. *Seeds* 5-7 mm, dark yellow or light brown, with a thin dark fissure line on each lateral face, arranged end-to-end in a single row, 5-9 per pod.

EXSICCATAE FROM CHILE AND PERU

CHILE: I REGION Arica, XII-1880, ORTEGA s.n. (SGO); Mantilla, s.d., HARMS s.n. (SGO); Mantilla, XI-1925, WERDERMANN 749 (K, SGO); Mantilla, XI-1925, WERDERMANN 750 (SGO); Mantilla, I-1903, REICHE s.n. (SGO); Valle de Azapa, 14 IX-1955, RICARDI 3322 (CONC); Quebrada de Chaca, 23 IX-1955, RICARDI 3457 (SGO); Mantilla (ca. 20°30'S-69°20'W),

1210 m, II-1989, ARONSON 7745 (CONC); Codpa (ca. 18°49'S-69°45'W), 1825 m, 13-II-1989, ARONSON 7762 (CONC); Valle de Chaca (ca. 18°40'S-70°15'W), 380 m, 13-II-1989, ARONSON 7764 (CONC); Valle de Chaca (ca. 18°40'S-70°15'W), 380 m, 13-II-1989; ARONSON 7768 (CONC, SGO); Valle de Azapa (ca. 18°25'S-70°23'W), 125 m, 14-II-1989, ARONSON 7775 (CONC, SGO).

PERU: Moquegua, moist banks of river valley, and sparingly along roadside (ca. 17°17'S-70°42'W), 1070 m, 16-II-1989, ARONSON 7781 (CONC, SGO); 18 km W of Mollendo, on road to Arequipa, (ca. 16°26'S-71°25'W), 3,800 m, dry hillside, 16-II-1989, ARONSON 7783 (CONC, SGO).

HABITAT AND ECOLOGY IN NORTHERN CHILE

Locally common in certain river valleys of the 1st Region, in dry to relatively moist sites near perennial and intermittent water courses, from sea level to approximately 1,200 m, *A. macracantha* appears to require a relatively high water table in order to survive in this arid region. It is nowhere very abundant, but as is the case for *Caesalpinia spinosa*, it can be supposed that the species would be much more abundant if trees were not regularly cut for firewood and browsed by roaming livestock, principally goats.

DISCUSSION

Unlike *Acacia caven*, whose occurrence in Chile is disjunct from the remainder of its area of distribution in Argentina, Bolivia, Paraguay, southern Brazil and western Uruguay (Aronson 1991) and whose present ecological behavior in Chile may be of relatively recent origin (Ovalle *et al.* 1990; Aronson 1991), populations of *A. macracantha* in northern Chile are essentially non-disjunct from similar stands in southern Peru. Like many members of subgenus *Acacia*, including *A. caven*, *Acacia macracantha* is quite variable in its distribution and ecological behavior. Thus in Hispaniola *A. macracantha* is very abundant and even dominant in a variety of xerophytic thornscrub associations partially or completely disturbed by man and domestic livestock. According to Barneby and Zanoni (1989, p. 11), "su distribución actual [in Hispaniola] probablemente resulta de la destrucción o la alteración de bosque seco y de la diseminación de sus semillas por ganado". A similar situation seems to prevail in parts of

southern Mexico and southern Venezuela (McVaugh 1987; Seigler and Ebinger 1988; Zapata and Kalin Arroyo 1978; Cárdenas and de Martino 1989). In contrast, in Peru, Ecuador, the Galapagos Islands, northeastern Columbia, dry northern Venezuela, and in some of the drier West Indian islands, this species appears to be rather rare, and generally confined to arid and semiarid zones including sand dunes (Macbride 1943; Wiggins and Porter 1971; Britton and Killip 1936; Correll and Correll 1982; Colonnello 1986). A similar distribution pattern has been noted for the species in southern Florida (Ward 1967), and it is this latter type of situation that characterizes the ecology of *A. macracantha* in northern Chile. In other words, where suitable moist, tropical or subtropical conditions exist, combined with human disturbance, *A. macracantha* occurs as a dominant element of secondary, deciduous thornscrub. In more arid areas, where anthropogenic disturbance may be even more intense and where hydric and edaphic resources are much more scarce, populations become rarer, smaller and reproductively insecure. As such, they may represent "peripheral isolates" from the main distribution area of their species (see Antonovics 1976). However, this interpretation should not exclude those populations from being considered part of the natural distribution of the species, any more than it has for isolated populations of this species in the Galapagos Islands, the Caribbean region, or southern Florida.

Accordingly, it seems appropriate to consider *Acacia macracantha* native to the 1st Region, and thus as a second *Acacia* species, after *A. caven*, found in Chile. It would however be prudent to employ the suffix "*sensu lato*", when discussing *A. macracantha* in Chile, since the taxonomic situation of this species is far from clear.

Highly variable throughout its range—as is *A. caven* (Aronson 1991)—*Acacia macracantha* has received contradictory treatment in various floras, wherein numerous varietal and specific names have been applied to plants of this "species". Bentham (1875) listed 14 synonyms, and the situation in this century has only scarcely improved (Spegazzini 1923; Isely 1973; Cialdella 1984; McVaugh 1987).

For example, on dry hillsides in a number of intermontane valleys in northern Peru, *A. macracantha* has differentiated sufficiently to

"earn a new name, *Acacia huarango* Ruiz ex Macbr. (Macbride 1943). But *A. macracantha* is reported from the same region (Weberbauer 1911), and *A. huarango* is distinguished from *A. macracantha* only by its more prostrate growth form and by having fewer pinnae per leaf (Macbride 1943). Similarly, in the Galapagos Islands, *A. macracantha* has apparently given rise to a small segregate species, *A. rorudiana* Christoph. with which it intergrades (Wiggins and Porter 1971). At present, both are considered well-established elements in five or six of the islands, though the suggestion is made that *A. rorudiana* may also occur on the South American mainland, in Chile (Wiggins and Porter 1971). [The specimens collected in 1880 by Ortega (SGO 30050, 30056, 30057) are perhaps the ones seen by these authors].

The major differences between *A. rorudiana* and *A. macracantha* as described by Christophersen (1931-32) are in width of the capitulum at anthesis and size of the leaflets. However, as in the case of the characters used to delimit *A. huarango*, these differences seem tenuous in view of the huge variability known in *A. macracantha*, and the well-developed phenotypic plasticity that leads to morphological variation in many acacias. For example, in discussing *A. farnesiana* in Australia, Pedley (1979) states: "Cultivated plants usually have larger leaves with more pinnae than described, while plants from arid areas have small leaves with few pinnae". I suspect that variations in leaf and inflorescence size traits, as well as life-form, another notoriously plastic trait, should not be considered sufficient to establish new binomials or even subspecific taxa in *A. macracantha* and other widespread acacias. Thus the distinction between *A. macracantha* and *A. tortuosa* (L.) Willd. (cf. Barneby and Zanoni 1989), usually drawn on the basis of leaf size and pinnae number, should be re-evaluated. To take another example, Cialdella (1984) gives number of pairs of pinnae in *A. macracantha* in Argentina as 8-12 whereas for *A. aroma*, she lists pinnae pairs 10-25. Yet the type specimen of *A. aroma* has 8-15 pairs of pinnae. Accordingly, this trait seems unsuitable for distinguishing between the two taxa.

A second suite of inter-related characters often used to split up or key out *A. macracantha* concerns the stipular spines. For example, in a

recent treatment of the acacias of Argentina, *A. macracantha* is noted as being "muy afin a *A. aroma*, de la que se diferencia por la morfología de las estipulas espinosas" (Cialdella 1984). Cialdella maintains that the spines of the former are rhomboid in cross section while those of *A. aroma* are round in cross section.

I suspect that some of confusion surrounding spine traits, in *A. macracantha* as in several other acacias, is due to incomplete herbarium specimens. On young branches where flowers and fruits are to be had, spines tend to be small, 2-5 mm. On larger branches and the trunk, by contrast, spines reach 40-65 mm and more (up to 90 mm in the West Indies (Adams 1972; Correll and Correll 1982)), but these are usually not collected. Similarly, spines on young twigs are round, while older ones are unmistakably flattened. This trait must also be considered with care.

In contrast with leaf, flower and spine traits, the pods of *A. macracantha* do seem useful in taxonomic diagnosis. To wit, the widespread element of northern Argentina, southern Bolivia and Paraguay known as *Acacia aroma* has fruits which are variable but almost always moniliform or necklace-shaped (Spegazzini 1923; Burkart 1952; Digilio and Legname 1966; Cialdella 1984; Tressans in prep.). Unfortunately, the type specimen of *A. aroma*, at Kew, and described by Hooker (1833), has no fruits.

Additional diagnostic features exist, however, between the plants generally considered pertaining to *A. aroma* and those assigned to *A. macracantha* as it is generally encountered west of the Andes and elsewhere in the Neotropics. These traits include seed color, pubescence, and intensity of cyanogenesis. Leaves of *Acacia macracantha* are not only much bigger than those of *A. aroma*, they are also usually quite pubescent. The seeds of *A. macracantha* are yellow while those of *A. aroma* are brownish-black. Finally, leaf samples of *A. macracantha* from Peruvian and several Central American collections consistently reveal the very strong presence of cyanogenic compounds, whereas most specimens of *A. aroma* tested to date in Argentina show no reaction (Aronson and Nash 1989) or very little (Seigler, *et al.* 1983; Aronson 1991). Moreover, the compounds found in the two taxa appear to be different: *A. macracantha* contains proacacipetalin, derived

from leucine, while *A. aroma* contains linamarin and lotaustalin, synthesized from the aliphatic amino acids valine and isoleucine (Seigler *et al.* 1978; Seigler and Conn 1982). Based on my own studies to date, *A. macracantha*, as the species is generally understood, probably does not occur in Argentina. However, the phylogenetic relationship between *A. aroma* and *A. macracantha* remains to be clarified, and it may well be that hybridization occurs between the two "species" if they do in fact overlap in Argentina, Peru, Paraguay, or Bolivia. Alternatively, it may ultimately prove necessary to combine these two "species" under a single binomial. Current studies in cyanogenesis and morphological variation (Seigler and Ebinger, pers. comm.) and in immunological and serological patterns in these groups (P. Brain, pers. comm.) may help sort out this question.

Further north, a bit of the inter-specific complexity involving *A. macracantha* is coming to light. In Mexico and Central America, *A. macracantha* appears to form part of a species complex which also involves *A. pennatula* (Schldl. & Cham.) Benth. and *A. cochliacantha* Humb. & Bonpl. ex Willd. (Seigler and Ebinger 1988), and introgressive hybridization takes place among all of them (Ebinger and Seigler 1987; Seigler and Conn 1982; Brimer *et al.* 1987; Seigler and Ebinger 1988). There is a notable lack of conformity, however, among authors dealing with Mexican material. For example, Seigler and Ebinger (1988) distinguish *A. macracantha* from *A. cochliacantha* by the round to oval cross-section of the spines of the former, compared to the flattened and "spoon-shaped" spines of the later. In contrast, McVaugh (1987) gives both species as having flattened spines, although only *A. cochliacantha* has "trough-shaped or boatshaped" mature spines. On the other hand, McVaugh (1987) describes the fruits of *A. macracantha* as occasionally being glabrous while those of the closely related *A. pennatula* are persistently pubescent, and lacking the transverse cracks or "stretch-marks" found in the pods of *A. macracantha*. This statement about fruits is confusing in view of the fact that the pod of Chilean and Peruvian material has "stretch-marks" and is always densely pubescent, thus corresponding to neither *A. pennatula* nor *A. macracantha*, sensu McVaugh (1987).

In Chile, as elsewhere, *Acacia macracantha* is

livestock-dispersed (personal observations) and, at times, an invasive weed in a variety of disturbed habitats (see Adams 1972; Chazaro Basañez 1977). These traits help explain its huge geographical distribution. Although the distribution and variation of *A. macracantha* in northern Chile is limited when compared to some other countries, its distribution and ecology there appears quite similar to that exhibited in other arid and semiarid regions further north. It remains to be seen whether the same morphological trends occur under arid conditions in widely separated regions.

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LITERATURE CITED

ADAMS, C.D. 1972. Flowering Plants of Jamaica. University of the West Indies. Mona, Jamaica. 848 pp.
 ANTONOVICS J. 1976. The Nature of limits to natural selection. *Ann. Missouri Bot. Gard.* 63:224-247.
 ARONSON, J. 1991. Evolutionary biology of *Acacia caven* (Leguminosae, Mimosoideae) I. Intraspecific variation. (*Ann. Missouri Bot. Gard.*, in review).
 ARONSON, J. and NASH R.J. 1989. Infrequent cyanogenesis in *Acacia caven* and notes on the importance of cyanogenic glycoside data in subgenus *Acacia*. *Bull. Int. Group Stud. Mimosoideae.* 17:97-110.
 BARNEBY, R.C. y T.A. ZANONI 1989. Las Acacias (*Acacia*, Mimosaceae) de la Española: dos nuevas, una mejor descrita, y una clave para todas, las indígenas así como las cultivadas. *Moscocosa* 5:4-27.
 BENTHAM, G. 1875. Revision of the Suborder Mimoseae. *Trans. Linn. Soc. London* 30:335-664. 5 pl.
 BRIMER, L., J.E. EBINGER, D.S. SEIGLER and J. VASSAL 1987. Cyanogenesis in *Acacia cochliacantha*. *Bull. Inter. Group Stud. Mimos.* 15:88-99.

BRENAN, J.P.M. 1970. *Flora Zambesiaca* Vol. 3, Part 1. Crown Agents for Overseas Governments and Administrations, London.
 BRITTON, N.L. and E.P. KILLIP 1936. *Mimosaceae and Caesalpiniaceae* of Colombia. *Ann. New York Acad. Sci.* 35:101-208, 2 pl.
 BURKART, A. 1952. *Las Leguminosas Argentinas, Silvestres y Cultivadas*. Acme, Buenos Aires. 2nd Ed.
 CHAZARO BASAÑEZ, M. 1977. El Huisache, *Acacia pennatulata* (Schlecht. & Cham.) Benth. Una invasora del centro de Veracruz. *Biotica* 2(3):1-18.
 CHRISTOPHERSEN, E. 1931-32. A Collection of plants from the Galapagos Islands. *Nyt Mag. Naturvidensk.* 70:67-96.
 CIADELLE, A.M. 1984. El género *Acacia* (Leguminosae) en la Argentina. *Darwiniana* 25(1-4):59-111.
 COLONNELLO, G. 1986. Plant communities of the island of Blanquilla Federal Dependencies Venezuela. *Mem. Soc. Ci. Nat. La Salle* 46(125-126):193-214.
 CORRELL D.S. and H.B. CORRELL 1982. *Flora of the Bahama Archipelago (Including the turks and Caicos Islands)*. J. Cramer. Vaduz.
 CARDENAS L. and G. de MARTINO 1989. El género *Acacia* en la Guyana Venezolana (Unpublished Manuscript, to appear in the forthcoming *Flora de la Guyana Venezolana*).
 DIGLIO A.P.L. y P.R. LEGNAME 1966. Los árboles indígenas de la provincia de Tucumán. *Opera Lilloana* XV.
 EBINGER, J.E. and SEIGLER, D.S. 1987. Introgressive hybridization in Mexican populations of *Acacia macracantha* and *Acacia pennatulata* (Fabaceae, Mimosoideae). *Bull. Int. Group Stud. Mimos.* 15:73-80.
 ELIAS, T.S. 1981. Mimosoideae. In R.M. Polhill & P.H. Raven (eds.) *Advances in Legume Systematics*, Vol. 1. Royal Botanical Gardens, Kew, U.K. pp.143-171.
 FOLLMANN, G. y V. MATTE 1963. Estepas sin jirafas. *Bol. Univ. Chile* 42:45-48.
 GUINET, P. and J. VASSAL 1978. Hypotheses on the differentiation of the major groups in the genus *Acacia*. *Kew Bull.* 32:309-336.
 HOOKER, W.J. 1833. *Botanica Miscellanea*, vol. 3. Royal Botanic Gardens, Kew, p. 206.
 ISELY, D. 1973. Leguminosae of the U.S. I. Subfamily Mimosoideae. *Mem. New York Bot. Gard.* 25:1-152.
 LIOGIER, A.H. 1985. La Flora de la Española. III. Universidad Central del Este. San Pedro de Macoris, República Dominicana.
 MARTICORENA, C. y M. QUEZADA 1985. Catálogo de la flora vascular de Chile. *Gayana, Bot.* 42:5-157.
 MACBRIDE, F. 1943. *Flora of Peru*. *Field Mus. Nat. Hist. Bot. Ser.* 13(1):81.
 MCVAUGH, R. 1987. *Flora Novo-Galiciana*. 5. Leguminosae. University of Michigan Press, Ann Arbor, USA.
 MUNOZ P.C. 1959. Sinopsis de la flora chilena. Ed. Univ. Chile, Santiago. 312 pp., 238 lam.
 OVALLE, C., J. ARONSON, A. DEL POZO, and J. AVENDAÑO 1990. The espinal: agroforestry systems of the mediterranean - type climate region of Chile: State of the art and prospects for improvement. *Agroforestry Systems* 10:213-239.

- PEDLEY, L. 1979. A revision of *Acacia* in Queensland. *Austrobaileya* 1:235-337.
- REICHE, K. 1905. Flora de Chile. Vol. 4. Imprenta Cervantes, Santiago.
- RICO ARCE, M. 1980. El género *Acacia* en Oaxaca (México). PhD Thesis, Univ. Fed. de México, D.F. México.
- RICO ARCE, M. 1984. El género *Acacia* en México. *Bull. Int. Group Stud. Mimosoideae* 12:50-59.
- RODRÍGUEZ, R., O. MATTHEI y M. QUEZADA 1984. Flora arbórea de Chile. Ed. Univ. de Concepción, Chile, 408 pp.
- ROSS, J.H. 1979. A conspectus of the African *Acacia* species. *Mem. Bot. Survey South Africa* N° 44. Depto. Agric. Tech. Services, Pretoria.
- SEIGLER, D.S., E.E. CONN, J.E. DUNN and G.L. HOLSTEIN 1978. Acaciapetalin from six species of *Acacia* from Mexico and Texas. *Phytochemistry* 17:445-446.
- SEIGLER, D.S. and E.E. CONN 1982. Cyanogenesis and systematics of the genus *Acacia*. *Bull. Int. Group Stud. Mimos.* 10:32-43.
- SEIGLER D.S., J.E. DUNN, E.E. CONN and J.F. PEREIRA 1982. Cyanogenic glycosides from four Latin American species of *Acacia*. *Biochem. Syst. Ecol.* 11:15-16.
- SEIGLER, D.S. and J.E. EBINGER 1988. *Acacia macracantha*, *A. pennatula*, and *A. cochliacantha* (Fabaceae: Mimosoideae) Species Complexes in Mexico. *Syst. Bot.* 13:7-15.
- SPEGAZZINI, C. 1923. *Acacias argentinas*. *Bol. Acad. Nac. Cienc. Córdoba* 26:161-334.
- STEYERMARK, J.A. and O. HUBER 1978. Flora del Avila. Flora y vegetación de las montañas del Avila, de la Silla y del Naiguatá. INCAFO, Madrid.
- TRESSENS, S. (in prep.) Arboles de la Provincia de Corrientes. Instituto de Botánica del Nordeste, ENNE-CONICET, Argentina.
- VASSAL, J. 1972. Apport des recherches ontogéniques et seminologiques à l'étude morphologique, taxonomique et phylogénique du genre *Acacia*. *Bull. Soc. Hist. Nat. Toulouse* 108:1-115.
- WARD, D.B. 1967. *Acacia macracantha*, a tree new to Florida and the United States. *Brittonia* 19:283-284.
- WEBERBAUER A. 1911. Die Pflanzenwelt der peruanischen Anden in ehren Grundzügen dorgestaellt. Wilhelm Engelmann, Leipzig.
- WIGGINS, I.L. and D.M. PORTER 1971. Flora of the Galapagos Islands. Stanford University, Stanford, California.
- WILLDENOW, K.L. 1806. *Acacia*. *Species Plantarum* 4(2):1080. G.C. Nauk, Berlin.
- ZAPATA, T.R. and M. KALIN ARROYO 1978. Plant reproductive ecology of a secondary tropical forest in Venezuela. *Biotropica* 10(3):221-230.